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Population consequences of migratory variability differ between flyways

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eTOC

Patchett et al. show that climate change, habitat loss and migration distance may influence population trends in migrant landbirds, but their relative effect varies between two major flyways.

Many populations of long distance migratory birds are declining, with candidate drivers including climate change shifting the location of suitable non-breeding habitat, outright anthropogenic habitat loss, or a combination of both [1]. The size of the non-breeding area over which a population spreads (migratory spread), and migration distance (or number of stop-over sites), however, may determine a species' susceptibility to such environmental change. Low migratory spread is predicted to increase vulnerability to climate-driven shifts in the location of suitable non-breeding habitat, because individuals are less likely to encounter newly suitable sites. All else being equal, outright loss of non-breeding habitat should result in population declines regardless of migratory spread. However, if migratory spread is low and habitat loss is uneven we would expect to sample some species which are experiencing habitat loss and some species which are not. In contrast, under high spread (or when habitat loss is evenly distributed), any sampled species is likely to experience habitat loss (Figure 1C). As migration distance increases so the probability of encountering a stop-over site with negative environmental change increases [3] (Figure 1D). Therefore, the presence of a positive relationship between species' population trends and migratory spread or a negative relationship between species' population trends and migration distance, should indicate whether climate-change-driven shifts in non-breeding habitat location, or environmental change at stopover sites, respectively, are likely drivers of migratory declines. These relationships may vary between flyways, which differ profoundly in their geography, climate variation and human population change. Here we show that migratory connectivity is correlated with migrant population trends and that low spread is associated with declining populations in the Neotropic flyway, but the reverse occurs in the Afro-Palearctic flyway. Thus climate change may be more important in Neotropic migrant population declines whereas habitat loss may be more important in the Afro-Palearctic.

We tested for relationships between species' population trends and their mean spread on the non-breeding ground, as well as their migration distance, and whether these relationships varied between the Neotropic and Afro-Palearctic flyways. We used all available published individual migration tracks (tracked from breeding to non-breeding grounds) of 875 adult landbirds from 122 populations of 48 species (Figure 1A and B) to calculate migratory spread (the mean inter-individual distance between birds from the same population on the non-breeding ground; data as in Finch et al. 2017 [4], with the addition of 17 more recent studies). We modelled each species' population status, using the most current IUCN assessment of declining, stable and increasing populations [5], against its non-breeding ground mean spread and mean distance of migration. We also included whether the species was in the Neotropic or Afro-Palearctic flyway, and interactions dependent on flyway, and controlled for the latitudinal zone of wintering (approximately the Caribbean and Central America versus South America, and Africa north and south of the equator), the longitude and latitude of the breeding population, and the phylogeny of the migratory species considered [4].

Scoring declining, stable and increasing populations as –1, 0 and 1, respectively, the mean population trend was –0.2 (47% of species declining, 27% increasing) in the Neotropic flyway and –0.55 (64% of species declining, 9% increasing) in the Afro-Palearctic flyway. In the Neotropic flyway, species with low spread (high connectivity) were significantly more likely to have declining populations ($t_{11.8}$ = 3.7, P<0.01), whilst in the Afro-Palearctic flyway, species with high spread (low connectivity) were more likely to have declining populations ($t_{27.7}$ = -2.2 P=0.033; interaction between flyway and migratory spread, $t_{41.3}$ = 3.9, P<0.001; Table S2, Figure 1G). In the Neotropic flyway, species with greater migratory distances were significantly more likely to have declining populations ($t_{9.1}$ = -3.5, P<0.01), whilst in the Afro-Palearctic flyway there was no relationship ($t_{27.4}$ = -0.2; interaction between flyway and migration distance, $t_{39.6}$ = -2.2, P=0.034; Table S2, Figure 1H). The fixed effects of flyway, migration distance and spread (and interactions between flyway and migration distance or spread), accounted for 30% of the variation in population trend, with phylogeny contributing an additional 5%. Migratory spread and migration distance accounted for 55% and 13% of variation in population trends in the Neotropic and Afro-Palearctic flyways respectively.

The positive correlation between population trend and migratory spread suggests that climate-change-driven shifts in the location of non-breeding habitat could be a driver of population declines in the Neotropic flyway. In contrast, there was a weak negative relationship between population trend and migratory spread in the Afro-Palearctic flyway, suggesting that habitat loss is occurring unevenly across Africa with a diluted impact on species with low spread. Long-term climatic conditions in South America may have been more stable in comparison to Africa [7], where climate varies across a continental scale between decades [6]. Migrant birds in the Afro-Palearctic flyway may then have already evolved generalist traits and a bet-hedging strategy of wide migratory spread in response [2]. Although habitat loss through land use change occurs in both flyways, human population growth (a reasonable proxy for rates of anthropogenic habitat transformation) has, and still is, occurring at a much greater rate in Africa but it is uneven and concentrated regionally (i.e. countries including and around Nigeria, and Uganda) [8]. The savannahs of sub-Saharan Africa, where most Afro-Palearctic species spend the non-breeding season, also have fewer protected areas than African tropical forests [9]. The differences between flyways in the effects of migration distance may then reflect current climate change and habitat loss in Central America and the Caribbean removing stop-over sites now, whereas at equivalent latitudes in Africa these were removed five thousand years ago with the formation of the Sahara [10].

Other factors acting on breeding and non-breeding grounds are also likely to be important drivers such as phenology mismatch [3]. Nevertheless, our results highlight how non-breeding migratory spread (migratory connectivity) might help explain general population trends of long-distance migrant birds, because migratory spread is likely to be an indication of a suite of bet-hedging adaptations to past variable climate and so a guide to future climate change responses, and how these might differ across flyways.

Author Contributions

All authors contributed equally to conceptualization, data collation, analysis and writing the paper.

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Supplemental Information

Document S1. Experimental Procedures and Two Tables

Declaration of Interests

The authors declare no competing interests.

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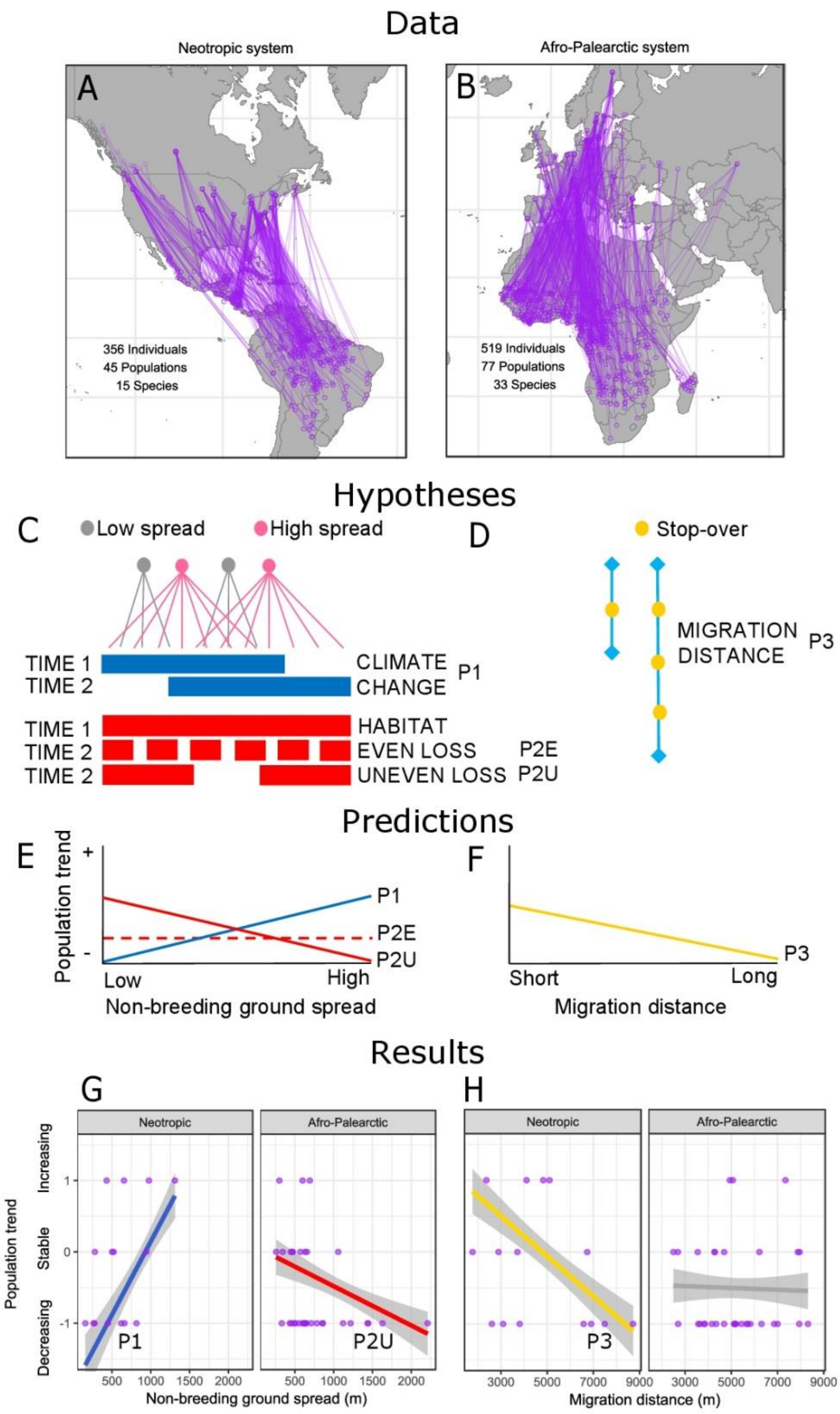
Figure 1.

Climate change, habitat loss and migration distance influence population declines in migrant landbirds, but their effect varies between two major flyways.

(A) Mercator projection of the Neotropic and (B) Afro-Palearctic migration systems showing breeding and non-breeding locations of all individuals used in analysis. (C) Representation of how species with low and high non-breeding ground spread (a measure of migratory connectivity) are predicted to be affected under scenarios of climate change shifting habitat or outright habitat loss (either evenly across range or uneven and localised into one main area) between two time periods. With climate change, high spread species are already spreading into shifted habitats as part of their bet-hedging strategy so there is no population change, whereas low spread species may now miss the shifted target habitat and show population declines. With outright habitat loss, however, all species are predicted to suffer declines, but if habitat loss is not even then habitat loss anywhere will always affect a high non-breeding spread population, but only those low non-breeding spread populations that have a range that encompasses the area of habitat change. Uneven habitat loss will therefore affect more high than low spread species. (D) Representation of how the number of stop-overs will increase with migration distance. As the number of stop-overs increases, so the probability of encountering the negative effects of climate change or habitat loss at any one of these stop-overs increases leading to population declines. (E) Predicted population trends in relation to non-breeding ground spread for climate change (P1) and habitat loss (even P2E and uneven P2U), and (F) in relation to migration distance (P3). (G) Observed relationships of population trend with non-breeding ground spread, and (H) migration distance. Lines in (G) and (H) are plotted from GLMMs ± 1SE; line colour corresponds to predictions in (E) and (F).



Data
Neotropic system
Afro-Palearctic system
A
B
356 Individuals
45 Populations
15 Species
519 Individuals
77 Populations
33 Species
Hypotheses
C
Low spread
High spread
TIME 1
TIME 2
CLIMATE
CHANGE
P1
TIME 1
TIME 2
TIME 2
HABITAT
EVEN LOSS
UNEVEN LOSS
P2E
P2U
D
Stop-over
MIGRATION
DISTANCE
P3
Predictions
E
Population trend
+
-
P1
P2E
P2U
Low
High
Non-breeding ground spread
F
P3
Short
Long
Migration distance
Results
G
Neotropic
Afro-Palearctic
Population trend
Increasing
Stable
Decreasing
1
0
-1
P1
P2U
500
1000
1500
2000
Non-breeding ground spread (m)
H
Neotropic
Afro-Palearctic
P3
3000
5000
7000
9000
Migration distance (m)

Supplementary Information: Population consequences of migratory variability differ between flyways

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SUPPLEMENTAL EXPERIMENTAL PROCEDURES

Migration Data

We used an updated version of the database in Finch *et al.* [S1] that contained breeding and wintering locations for 875 individuals, from 122 populations of 48 species (see Table S1 and Supplementary References for all studies used in analysis). Data came from a comprehensive search of peer-reviewed tracking studies for all European and North American species classed (according to BirdLife; http://www.birdlife.org/datazone/species/search) as migratory land-birds by entering the terms [latin name] AND migra* AND (gps OR geolo* OR satellite) into the Web of Science online library. From these studies, breeding and non-breeding (i.e. the site where an individual spent the majority of the wintering, non-breeding period after migration) locations of individual birds were extracted (or approximated from plotted map locations using Google Earth when precise coordinates were not given).

Our data are prone to two potential sources of error; imprecision in the translation of data from published figures to latitude-longitude coordinates via Google Earth (‘translation error’), and inaccuracy of solar geolocator-derived positions in the original published data (‘geolocator error’). The sensitivity of our results to these sources of error was fully explored in Finch *et al.* [S1]. Results were little affected suggesting that errors were unbiased, and effects were relatively small and so are not considered further.

As in Finch *et al.* [S1], we restricted our study to the autumn (fall) migration of adult birds that were tagged on the breeding ground; we removed species with a sample size of one; we defined the Afro-Palearctic system as populations breeding in Europe west of 65°E that have a non-breeding area in Africa south of 20°N; we defined the Neotropic system as all populations breeding in North America with a non-breeding area south of 30°N; we split each systems’ non-breeding area into northern and southern zones based on the distinct change in land to sea ratio (split at 12°N in the Neotropic and 4°N in the Afro-Palearctic system); and we classed birds tagged within 100 km of each other as coming from the same population. Where there was more than one non-breeding site reported for an individual, we selected the non-breeding location based on length of stay (i.e. identifying the main wintering area), unless that information was unavailable when we selected the first reported non-breeding site. Of the 875 individual birds used for analysis, only 40 were reported to have wintered in more than one location.

We used the mean pairwise great circle distance between non-breeding locations for individuals from the same population as a measure of population spread (as in Finch *et al.* [S1]). We then calculated mean species-level spread (referred to as *spread*) from these measures of mean spread, averaged across all populations sampled for each species.

We used the mean great circle distance between the breeding and non-breeding locations for individuals from the same population to calculate a measure of migration distance (as in Finch *et al.* [S1]). We calculated mean species-level migration distance from these measures of migration distance, averaged across all populations sampled for each species.

Population Trend

We used species-level population trend data (*increasing, stable*, *decreasing* or *unknown*) published online by BirdLife International [S2] to classify a trend for each species where we could calculate mean species non-breeding spread (Table S1). Species with *unknown* trend were omitted from analysis.

Statistical Analysis

We used GLMMs to explore the extent to which population trend (*increasing, stable*, *decreasing* coded as 1, 0, -1 respectively) depends on spread and migration distance, with the total sample size reflecting the number of each different species in the two flyways (N = 48). We included fixed effects for spread (we transformed spread using the natural logarithm to ensure normally distributed residuals), migration distance (great circle distance between mean breeding and non-breeding sites), breeding longitude and latitude (centred for each system), zone and system. Continuous predictor variables were centred and scaled. We also included interactions between system and migration distance, and system and species spread. To test for higher level effects of taxonomy we included a random effect of family nested within order. Models were fitted using the Lme4 package in R. Model fit was assessed by visual inspection of residuals plotted against fitted values and quantile plots. Full models including all terms of interest and confounding variables and minimum adequate models including only significant terms were compared and gave similar results (Table S2).

Table S1. All species used in analysis with respective population trend from BirdLife International [S2].

Species (common name)	Family	Order	Population trend	System	References
Alpine swift	Apodidae	Apodiformes	stable	Afro-Palearctic	[S3]
Aquatic warbler	Acrocephalidae	Passeriformes	decreasing	Afro-Palearctic	[S4]
Barn swallow	Hirundinidae	Passeriformes	decreasing	Afro-Palearctic	[S5]
Common cuckoo	Cuculidae	Cuculiformes	decreasing	Afro-Palearctic	[S6,S7]
Common nightingale	Muscicapidae	Passeriformes	stable	Afro-Palearctic	[S8]
Common nightjar	Caprimulgidae	Caprimulgiformes	decreasing	Afro-Palearctic	[S9–S11]
Common redstart	Muscicapidae	Passeriformes	increasing	Afro-Palearctic	[S12]
Common swift	Apodidae	Apodiformes	stable	Afro-Palearctic	[S13–S16]
Cyprus wheatear	Turdidae	Passeriformes	stable	Afro-Palearctic	[S17]
Egyptian vulture	Accipitridae	Accipitriformes	decreasing	Afro-Palearctic	[S18,S19]
Eleonora’s falcon	Falconidae	Accipitriformes	increasing	Afro-Palearctic	[S20–S22]
European hoopoe	Upupidae	Bucerotiformes	decreasing	Afro-Palearctic	[S23,S24]
European roller	Coracidae	Coraciiformes	decreasing	Afro-Palearctic	[S25]
Great reed warbler	Acrocephalidae	Passeriformes	decreasing	Afro-Palearctic	[S26,S27]
Hobby	Falconidae	Accipitriformes	decreasing	Afro-Palearctic	[S28,S29]
Honey buzzard	Accipitridae	Accipitriformes	decreasing	Afro-Palearctic	[S30]
House martin	Hirundinidae	Passeriformes	decreasing	Afro-Palearctic	[S31]
Lesser kestrel	Falconidae	Accipitriformes	stable	Afro-Palearctic	[S32,S33]
Lesser spotted eagle	Accipitridae	Accipitriformes	stable	Afro-Palearctic	[S34]
Marsh harrier	Accipitridae	Accipitriformes	increasing	Afro-Palearctic	[S35]
Montagu’s harrier	Accipitridae	Accipitriformes	decreasing	Afro-Palearctic	[S36–S38]
Northern wheatear	Muscicapidae	Passeriformes	decreasing	Afro-Palearctic	[S39,S40]
Ortolan bunting	Emberizidae	Passeriformes	decreasing	Afro-Palearctic	[S41,S42]
Pallid harrier	Accipitridae	Accipitriformes	decreasing	Afro-Palearctic	[S43]
Pied flycatcher	Muscicapidae	Passeriformes	decreasing	Afro-Palearctic	[S44]
Red-backed shrike	Laniidae	Passeriformes	decreasing	Afro-Palearctic	[S45,S46]
Sand martin	Hirundinidae	Passeriformes	decreasing	Afro-Palearctic	[S31]
Semi-collared flycatcher	Muscicapidae	Passeriformes	decreasing	Afro-Palearctic	[S47]
Short-toed eagle	Accipitridae	Accipitriformes	stable	Afro-Palearctic	[S48,S49]
Tawny pipit	Motacillidae	Passeriformes	stable	Afro-Palearctic	[S50]
Thrush nightingale	Muscicapidae	Passeriformes	stable	Afro-Palearctic	[S51]
Turtle dove	Columbidae	Columbiformes	decreasing	Afro-Palearctic	[S52,S53]
Willow warbler	Phylloscopidae	Passeriformes	decreasing	Afro-Palearctic	[S54]
Bullocks oriole	Icteridae	Passeriformes	stable	Neotropic	[S55]
Blackpoll warbler	Parulidae	Passeriformes	decreasing	Neotropic	[S56]
Bobolink	Icteridae	Passeriformes	decreasing	Neotropic	[S57]
Broad-winged hawk	Accipitridae	Accipitriformes	increasing	Neotropic	[S58]
Eastern kingbird	Tyrannidae	Passeriformes	decreasing	Neotropic	[S59]
Gray catbird	Mimidae	Passeriformes	stable	Neotropic	[S60]
Northern black swift	Apodidae	Apodiformes	decreasing	Neotropic	[S61]
Osprey	Pandionidae	Accipitriformes	increasing	Neotropic	[S62–S65]

Ovenbird	Parulidae	Passeriformes	stable	Neotropic	[S66,S67]
Purple martin	Hirundinidae	Passeriformes	stable	Neotropic	[S68]
Red-eyed vireo	Vireonidae	Passeriformes	increasing	Neotropic	[S69]
Scissor-tailed flycatcher	Tyrannidae	Passeriformes	decreasing	Neotropic	[S59]
Veery	Turdidae	Passeriformes	decreasing	Neotropic	[S70,S71]
Western kingbird	Tyrannidae	Passeriformes	increasing	Neotropic	[S59]
Wood thrush	Turdidae	Passeriformes	decreasing	Neotropic	[S72]

Table S2. Full and best model summary table. w.spread = non-breeding mean spread; mig.distance = distance of migration; system = Neotropical or Palearctic flyway; zone = location of non-breeding ground in either Central or South America, or Africa approximately above and below the equator; b.lon.rel = scaled mean breeding longitude; b.lat.rel = scaled mean breeding latitude.

	Parameter estimate													
Model	*Intercept*	*Log (w.spread)*	*mig. distance*	*system*	*zone*	*b.lon.rel*	*b.lat.rel*	*mig. distance x system*	*w.spread x system*	k	AICc	Delta	R^2m	R^2c
1	-0.50	-0.26	-0.026	0.46				-0.42	0.80	9	100.1	0	0.30	0.35
2	-0.47	-0.27	-0.0056	0.49	-0.082	0.00023	0.000097	-0.42	0.81	14	106.5	6.4	0.29	0.34

Supplemental References

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